

Reproductive Anatomy of *Vespericola shasta*
(Berry, 1921) (Gastropoda: Pulmonata: Polygyridae),
and Descriptions of Two New Species of *Vespericola*
from Northern California

by

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Abstract. The reproductive anatomy of *Vespericola shasta* (Berry, 1921) is described. Two new species, *Vespericola rothi* and *Vespericola scotti*, are described and compared to *V. shasta* and to other *Vespericola* species with somewhat similar anatomies.

INTRODUCTION

Roth & Miller (1993) presented the first of a series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. Here we present the results of an investigation of the anatomy of topotypes of *Vespericola shasta* (Berry, 1921) and of the identity of four other vicinal populations.

Vespericola shasta was described by S. Stillman Berry on the basis of shell characters only. The type locality was given as La Moine, Shasta County, California. *Vespericola* populations from nearby localities (Flume Creek and 22 km from Sacramento River bridge on road from Volmer to McCloud River bridge), whose shells resembled those of *V. shasta*, were collected several years ago by one of us (W.B.M.) and provisionally catalogued as *V. shasta*. Upon examination of their anatomies, however, it was obvious that we had collected two very different species.

In order to determine which one, if either, was the real *Vespericola shasta*, it was necessary to obtain topotype specimens and examine their anatomies. One of us (W.B.M.) collected presumed topotypes from La Moine on 13 April 1994. There are two creeks at La Moine, Slate Creek and Little Slate Creek, which empty separately into the Sacramento River within 300 m of each other, and both had *Vespericola* populations. The locality at Little Slate Creek at La Moine most closely resembled the description of the type locality given by Berry; additionally, the shells of its *Vespericola* population were more similar to the holotype and paratypes than those from Slate Creek. Accordingly,

specimens from Little Slate Creek at La Moine were regarded as topotypes.

The specimens from Slate Creek and Flume Creek had anatomies similar to that of *Vespericola shasta* topotypes and are therefore considered to be *V. shasta*. This extends the range of the species by about 15 km to the north of La Moine. To determine if the range extended westward, specimens from a population of *Vespericola* from the Coffee Creek drainage, tributary to the Trinity River, about 35 km to the west of La Moine, were also dissected and examined. Their anatomies showed that they were a new species, described below as *Vespericola scotti*. Specimens from 22 km from the Sacramento River bridge on the road from Volmer to McCloud River bridge, roughly 15 km to the east of La Moine, collected and dissected in 1969, were also a new species. Fresh specimens from that locality could not be collected, however, because of road conditions, but specimens from a nearby population, with similar anatomies, were obtained and examined and are described below as *Vespericola rothi*.

MATERIALS AND METHODS

Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of Pilsbry (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 40× magnification under a dissecting mi-



Explanation of Figures 1 to 9

Figures 1-3. *Vespericola shasta* (Berry). Holotype, SBMNH 34131, California: Shasta County: La Moine, A. G. Smith coll., August 1921. Top, apertural, and basal views. Diameter 13.3 mm. Figures 4-6. *Vespericola scotti* Cordero & Miller, sp. nov. Holotype, SBMNH 142559, California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994. Top, apertural, and basal views. Diameter 12.8 mm. Figures 7-9. *Vespericola rothi* Cordero & Miller, sp. nov. Holotype, SBMNH 142560, California: Shasta County: along banks of Ellery Creek, near its confluence with Lake Shasta, under logs in briars, W. B. Miller coll., 27 May 1994. Top, apertural, and basal views. Diameter 16.4 mm. (This shell, selected as holotype, was originally numbered 142094-D; photograph taken prior to number change.)

croscope with an ocular reticle. Three counts were taken per specimen, and the mean (to the nearest integer) recorded.

Specimens for dissection were prepared by the method of Miller (1967). Snails were first drowned in water to ensure expansion and relaxation, then heated to a temperature of 60°C, at which time the bodies could be pulled easily from the shells and dissected. After the body cavity was opened, the position and maturity of the reproductive system were observed; then the whole reproductive system was removed, attached to a small patch of body wall around the external genital orifice. The penis was slit longitudinally to expose the verge of at least one specimen from each locality.

Whole mounts of genitalia were prepared by the method of Miller (1967): stained with hematoxylin and eosin, dehydrated and cleared in successive baths of ethanol and toluene, and mounted on slides with Permount mounting medium. Organ measurements were taken from dissected specimens. Anatomical drawings were made by projecting the image of the whole mount on paper with an overhead projector.

Shell growth in Polygyridae is determinate and ends with, first, a constriction of the body whorl and then a turning outward and thickening of the lip. Reproductive maturity normally seems to follow a short time after the lip turns, but the presence of a turned lip does not guarantee a reproductively mature specimen. Therefore, at least a portion of each sample was kept alive in a terrarium for a period of weeks or months to ensure full development of the genital structures. Terraria consisted of redwood boxes with screened tops. A 3–6 cm layer of soil and leafmold from the collecting locality was added. Specimens were fed lettuce. There is no indication that growth of *Vespericola* in terraria under these conditions is in any way abnormal.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History.

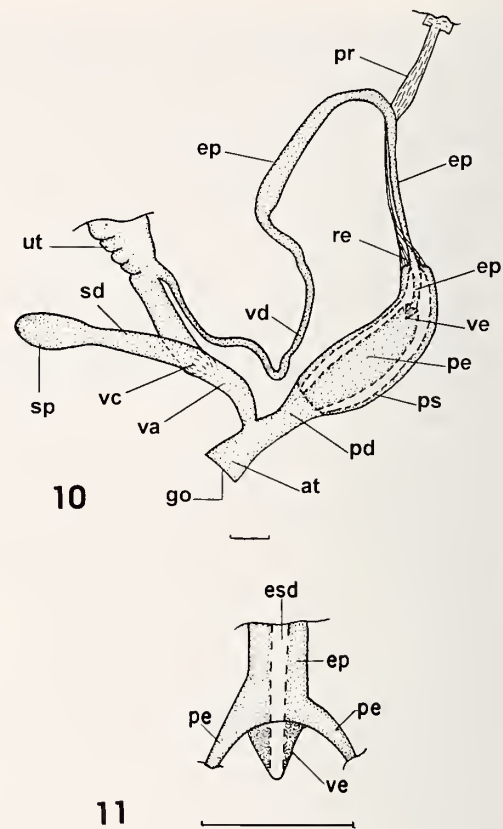
SYSTEMATICS

Vespericola shasta (Berry, 1921)

(Figures 1–3, 10–11)

Polygyra columbiana shasta Berry, 1921:37, pl. 2, figs. 6, 7.
Vespericola shasta (Berry), Pilsbry, 1939:903–904, figs. 518d, 518d', 518f, 518g.

Diagnosis: A small *Vespericola* with depressed-helicoid to conical, moderately umbilicate shell, usually with a parietal lamella, those from the type locality mostly smooth, glossy, and without periostracal setae; a few shells with about one or two setae/mm². Shells from conspecific vicinal populations with four to seven periostracal setae/mm². Penis elongate-conical, entirely enclosed by the penial



Explanation of Figures 10 and 11

Figures 10, 11. *Vespericola shasta* (Berry). Drawings made from projections of stained whole mounts of topotypes. Figure 10. Anterior portion of reproductive system, SBMNH 142066, California: Shasta County: La Moine: Little Slate Creek: in leafmold-covered rocks above edge of creek on right bank, W. B. Miller coll., 13 April 1994. Figure 11. Part of epiphallus and apical end of penis opened to show verge, SBMNH 142066, collection data same as above. Abbreviations for anatomical figures: at, atrium; ep, epiphallus; esd, epiphallic seminal duct; go, genital orifice; lu, lumen of epiphallic seminal duct; ov, oviduct; pe, penis; pd, peduncle; pr, penial retractor; ps, penial sheath; re, retentor; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vc, vaginal collar; vd, vas deferens; ve, verge. Scale lines in anatomical figures = 1 mm.

sheath, which also encloses part of the proximal epiphallus; verge 0.2 to 0.3 mm long, conical, with seminal duct opening at the blunt tip.

Description of holotype: Shell medium-sized for the genus (diameter 13.3 mm) broadly conical, narrowly umbilicate, with 5¾ whorls. Spire weakly convex; whorls rounded, suture strongly impressed. Embryonic whorls indistinguishable from later whorls. Sculpture consisting of numerous and fairly strong rugae, much weaker on the base; surface polished and lustrous, without periostracal

setae. Periphery smoothly rounded. Base tumid, lustrous. Umbilicus contained about 12 times in diameter. Body whorl deflected downward, slightly constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile. Lip turned outward and expanded, somewhat reflected at base. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly dilated, covering one-third of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: Nine topotypes from Little Slate Creek, La Moine, California, were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, completely enclosed in thin sheath adnate to base (Figure 10). Short, peduncular portion of about 0.6 mm present between base of the sheath and the junction with the atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing minuscule conical pointed verge varying from 0.2 to 0.3 mm long and 0.2 to 0.3 mm wide at its base. Seminal duct opening into penial chamber at cleft tip of verge (Figure 11).

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to the summit of the penial sheath, from which other retentor fibers form connections with parts of the epiphallus and vas deferens.

In the nine topotypes, sheath length varying from 4.2 to 5.7 mm, with mean of 4.6 mm. On average, sheath extending 1.1 mm beyond apical end of penis.

Spermathecal duct narrow, tightly appressed to free oviduct (which is smaller in diameter and branches from it), about 2.6 mm long, about 0.6 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 1.9 mm long and 1.3 mm in diameter, with bluntly pointed tip.

Slight swelling on vagina present at junction of spermathecal duct and oviduct in most dissected topotypes.

Type material: Holotype: SBMNH 34131. Paratypes: SBMNH 34132. Paratypes also deposited by the author in the collections of the CAS, ANSP, and Leland Stanford Junior University, as well as the private collection of Allyn G. Smith, subsequently also deposited in the CAS.

Distribution: Shasta County, California, along Flume Creek near its confluence with the Sacramento River and at La Moine, along Slate Creek and Little Slate Creek near their confluences with the Sacramento River.

Remarks: The type locality of *Vespericola shasta* is La Moine, with no more exact location specified. At La Moine, two creeks, Slate Creek and Little Slate Creek, empty

directly into the Sacramento River within 300 m of each other. Slate Creek is the larger creek, with steep banks and swiftly flowing water, offering very little shelter at the water's edge. Only three live specimens were collected along Slate Creek, while about 20 were collected at Little Slate Creek. Allyn G. Smith, who collected the type lot of 25 specimens in August 1921 found them "almost in the water under sticks and stones" (Berry, 1921). Furthermore, Berry emphasized that the features which served to set this species quite distinctly apart were its warm brown color, smooth, polished surface, lack of any sort of persistent periostracal fringes, and narrow, though permeable umbilicus. The specimens from Little Slate Creek reflect all of these characters, while those from Slate Creek had persistent periostracal setae, about 4–7/mm². Although this character is considered insufficient to suggest reproductive isolation and speciation, it does serve to narrow down the type locality to Little Slate Creek. Accordingly, specimens from Little Slate Creek are considered topotypes. The two specimens from Slate Creek had anatomies which showed no significant differences from those from Little Slate Creek and are therefore considered to be conspecific.

Two specimens from Flume Creek, which empties into the Sacramento River about 15 km to the north, also had persistent periostracal setae about 1–3/mm². Other shell characters, as well as anatomical characters, were similar to those of Little Slate Creek and therefore this population is considered to be conspecific, thereby extending the range of the species northward to Flume Creek.

Anatomically, *Vespericola shasta* is distinguished from other species by its penial sheath, which not only encloses the entire penis, but also a portion of the proximal epiphallus, and by its minuscule, conical, pointed verge.

Vespericola scotti Cordero & Miller, sp. nov.

(Figures 4–6, 12–13)

Diagnosis: A small to medium-sized *Vespericola* with depressed-helicoid to broadly conical, narrowly umbilicate shell, 5½ to 5¾ whorls, 3–12 periostracal setae/mm², usually with a parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.3; verge minuscule, consisting only of a rim papilla at the tip of the epiphallus, about 0.1 mm high, barely protruding into the penial chamber.

Description of shell: Shell small to medium-sized for the genus (diameter 11.2 to 13.1 mm) depressed-helicoid to broadly conical, narrowly umbilicate, with 5½ to 5¾ whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae. Periostracum bearing slender setae, 3–12/mm² on shoulder of body whorl. Surface between setae densely, smoothly granulose on spire and body whorl and collabrally wrinkled. Periphery simply rounded. Base

tumid, smooth. Umbilicus contained about 15–21 times in diameter. Body whorl deflected downward, slightly constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile. Lip turned outward and expanded, somewhat reflected at base. Parietal lamella usually present. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering one-half to three-fourths of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: The holotype and 18 paratypes were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, anterior, basal part enclosed in thin sheath adnate to base; protruding part stout and markedly curved. Short, peduncular portion of about 0.9 mm present between base of sheath and junction with atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing minuscule verge consisting of a circular, protruding papilla at tip of seminal duct, insufficiently long to converge into a pointed tip, 0.1 mm long and 0.3 mm wide at its base, the perimeter of the seminal duct (Figure 13).

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to summit of penial sheath, from which other retentor fibers form connections with parts of epiphallus and vas deferens.

Sheathed part of penis in the holotype about 5.2 mm in length; protruding part about 4.6 mm long. In the 18 paratypes, sheath length varying from 2.5 to 5.8 mm, with mean of 4.6 mm; protruding part varying from 4.1 to 7.8 mm in length, with mean of 6.0 mm. Mean ratio of protruding length to sheathed length about 1.3.

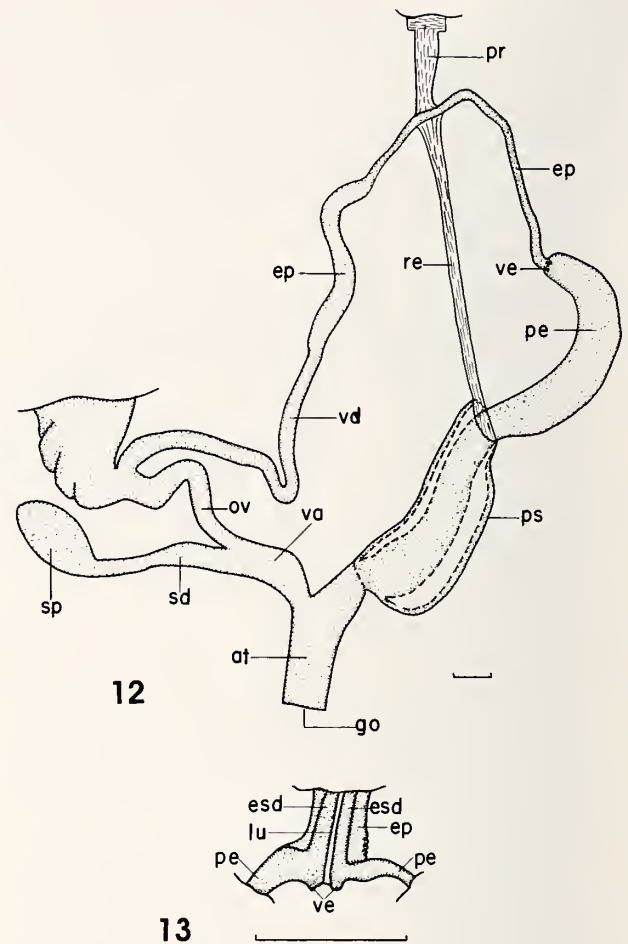
Spermathecal duct moderately swollen at base where it joins oviduct, tightly appressed to free oviduct, about 2.6 mm long, tapering from about 0.7 mm diameter at junction with oviduct to 0.3 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 2.6 mm long and 1.3 mm in diameter, with bluntly pointed tip.

Type material: Holotype: SBMNH 142559 (shell and stained whole mount of reproductive system), California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994.

Paratypes: SBMNH 142084 (12 shells and stained whole mounts of reproductive system), from same locality as holotype. Additional paratypes deposited in ANSP and FMNH.

Distribution: This species is currently known only from the type locality.



Explanation of Figures 12 and 13

Figures 12, 13. *Vespericola scotti* Cordero & Miller, sp. nov. Drawings made from projections of stained whole mounts of paratypes. Figure 12. Anterior portion of reproductive system, SBMNH 142084, California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994. Figure 13. Longitudinal section of junction of epiphallus with penis, showing verge papilla, SBMNH 142084, collection data same as above. Abbreviations for anatomical figures as for Figures 10, 11. Scale lines in anatomical figures = 1 mm.

Remarks: By shell characters, *Vespericola scotti* is difficult to separate from populations of *V. shasta* that have sparse periostracal setae such as those from Slate Creek and Flume Creek.

Anatomically, however, *Vespericola scotti* differs from all other known species of *Vespericola* by its verge which consists only of a minuscule rim papilla at the end of the epiphallus, about 0.1 mm in height, barely protruding into the penial chamber, insufficiently long to converge into a conical tip. Its recurved, stout and long protruding penis also separates it from other species.

Vespericola scotti has been found only in a very limited

habitat, along the edge of a small running stream descending steeply in Benson Gulch about 500 m from its confluence with Coffee Creek. The majority of living adults were found under large pieces of alder bark that were kept partially wet by the stream water. The dominant trees in the gulch are Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and incense cedar (*Calocedrus decurrens*), with an understory of big leaf maple (*Acer macrophyllum*), red alder (*Alnus oregona*), and Pacific dogwood (*Cornus nutallii*).

Etymology: This species is named for Paul Scott of the SBMNH, who made it possible for us to collaborate and assisted us greatly in the preparation of this article.

Vespericola rothi Cordero & Miller, sp. nov.

(Figures 7–9, 14–15)

Diagnosis: A medium-sized to large *Vespericola* with depressed-helicoid to broadly conical, widely umbilicate shell, the umbilicus nearly half-covered by the columnella, 5¾ to 6 whorls, 2–7 periostracal setae/mm², without parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.0; verge 0.5 mm long, conical, ending in a blunt tip. Conspicuous swelling on vagina at junction with spermathecal duct and oviduct.

Description of shell: Shell medium-sized to large for genus (14.2 to 16.9 mm in diameter) depressed-helicoid to broadly conical, widely umbilicate, with 5¾ to 6 whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae. Periostracum bearing slender, sparse setae, 2–7/mm² on shoulder of body whorl. Surface between growth wrinkles microscopically granulose. Periphery simply rounded. Base tumid, smooth. Umbilicus contained about 13–16 times in diameter, with persistent periostracal setae and papillae. Body whorl deflected downward, moderately constricted behind lip. Aperture roundly lunate; peristome shallowly concave in profile. Lip narrowly reflected, somewhat thickened at base. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering one-fourth to one-half of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: The holotype and three paratypes were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, anterior, basal part enclosed in thin sheath adnate to base. Short, peduncular portion of about 1.1 mm present between base of sheath and junction with atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing short, conical pointed verge 0.5 mm long and 0.5 mm wide

at its base. Seminal duct opening into penial chamber at cleft tip of verge.

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to summit of penial sheath, from which other retentor fibers form connections with parts of epiphallus and vas deferens.

Sheathed part of penis in the holotype about 7.0 mm in length; protruding part about 5.5 mm in length. In the three paratypes, sheath varying from 5.1 to 7.0 mm in length, with mean of 5.9 mm, protruding part varying from 5.2 to 7.0 mm in length, with mean of 5.9 mm. Mean ratio of protruding length to sheathed length about 1.0.

Spermathecal duct moderately wide, tightly appressed to free oviduct (which is smaller in diameter and branches from it), about 4.6 mm long, gradually tapering from about 1.2 mm in diameter at junction with oviduct to 0.6 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 5.9 mm long and 3.0 mm in diameter, with bluntly pointed tip.

Conspicuous swelling on vagina at junction of spermathecal duct and oviduct in all dissected types.

Type material: Holotype: SBMNH 142560 (shell and dissected anatomy), California: Shasta County: Ellery Creek about 200 m from its confluence with Lake Shasta, W. B. Miller and B. Roth coll. 27 May 1994.

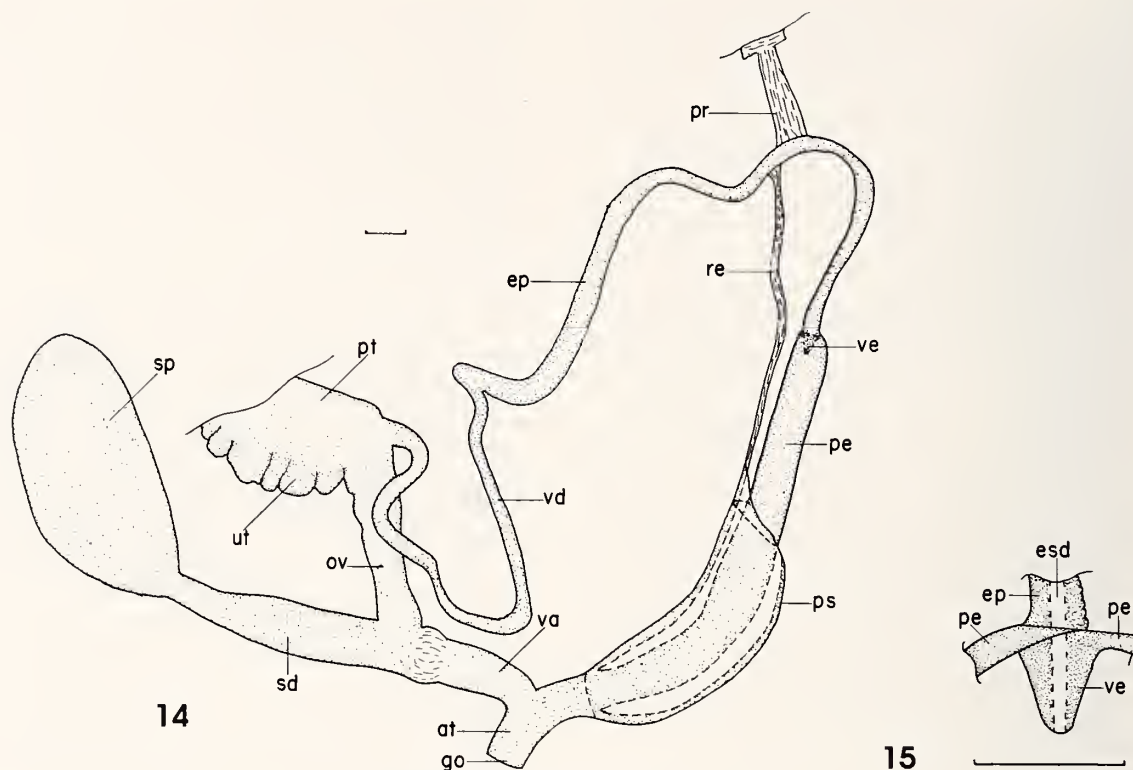
Paratypes: SBMNH 142094 (3 shells and stained whole mounts of reproductive system), from same locality as holotype.

Referred material: California: Shasta County: Along road from Volmer to McCloud River bridge at a ravine 22 km from Sacramento River bridge. SBMNH 75185 (20 shells and 2 stained whole mounts of reproductive system); W. B. and W. N. Miller coll., 15 August 1969.

Distribution: Shasta County, California, along lower end of Ellery Creek and along unnamed limestone ravine with running stream along old road from Volmer to McCloud River bridge about 22 km from Sacramento River bridge.

Remarks: The specimens listed above under Referred Material consisted of 18 living adults which were actively crawling along the wet edge of a small stream in an unnamed limestone ravine along the road. In shell size (11.3 to 14.7 mm in diameter) they are markedly smaller than the types from Ellery Creek; the umbilicus is relatively wide, contained 10–13 times in the diameter and similarly covered one-fourth to one-half by the inner lip; the shells are smooth and glossy, without periostracal setae. Anatomically, they are similar in all respects to the types except for being proportionally smaller.

The absence of periostracal setae in this population versus their sparse occurrence (2–7/mm²) in the type population mirrors the situation in *Vespericola shasta* for populations from the type locality, Little Slate Creek, versus



Explanation of Figures 14 and 15

Figures 14, 15. *Vespericola rothi* Cordero & Miller, sp. nov. Drawings made from projections of stained whole mounts. Figure 14. Anterior portion of reproductive system of holotype, SBMNH 142560, California: Shasta County: along banks of Ellery Creek, near its confluence with Lake Shasta, under logs in briars, W. B. Miller and B. Roth coll., 27 May 1994. Figure 15. Part of epiphallus and apical end of penis opened to show verge of paratype. SBMNH 142094, collection data same as above. Abbreviations for anatomical figures as for Figures 10, 11. Scale lines in anatomical figures = 1 mm.

those from Slate Creek and Flume Creek. Furthermore, instances of marked disparity in shell diameter between populations of the same species of *Vespericola* have been observed in *Vespericola marinensis* Roth & Miller, 1993, as well as in *Vespericola columbianus* (Lea, 1838), *Vespericola megasoma* (Pilsbry, 1928), and *Vespericola euthales* (Berry, 1939) (Roth & Miller, unpublished observations).

Accordingly, the specimens from this unnamed limestone ravine are considered to be conspecific with the Ellery Creek types.

Vespericola rothi exhibits anatomical characters similar to those of *Vespericola pressleyi* Roth, 1985, in that the penis is long, with a protruding part to sheathed part ratio of about 1.0, and the verge is short, conical, and about 0.6 mm long. In *V. pressleyi*, however, the entire penis is markedly thin, about 0.5 mm in diameter along its entire length almost to the base where it abruptly widens to a base diameter of 0.9 to 1.0 mm. In *V. rothi*, the penis is stout, cylindrical for its entire length, about 1.0 mm in diameter. Additionally, *V. pressleyi* consistently has a massive spermathecal duct, about 1.4 mm in diameter at its junction

with the oviduct and no enlarged vaginal collar; *V. rothi*, however, has a relatively thin spermathecal duct, 1.1 mm at its base, and a large vaginal collar is present in all specimens dissected.

Vespericola rothi differs from *Vespericola pressleyi* and other known species of *Vespericola* in shell characters by its wide umbilicus which is one-fourth to one-half covered by the reflected columellar lip; in *V. pressleyi*, the inner lip is not markedly dilated over umbilicus (Roth, 1985).

Vespericola rothi appears to be an obligate calcicole, living only at the water's edge in limestone ravines. *Vespericola pressleyi*, in contrast, has been found in large numbers in acidic humus under decaying fir logs near its type locality close to Big Bar Ranger Station, Trinity County, California.

The vegetation along lower Ellery Creek consisted primarily of willows with intertwining blackberry vines and stinging nettles so thick as to make the area almost impassable.

Etymology: The species is named for Dr. Barry Roth who

suggested and led the expedition to Ellery Creek in his continuing effort to study the speciation and distribution patterns of *Vespericola*.

ACKNOWLEDGMENTS

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